



Disentangling the *Pelomedusa* complex using type specimens and historical DNA (Testudines: Pelomedusidae)

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Abstract

Recent research has shown that the helmeted terrapin (*Pelomedusa subrufa*), a species that occurs throughout sub-Saharan Africa, in Madagascar and the southwestern Arabian Peninsula, consists of several deeply divergent genetic lineages. Here we examine all nominal taxa currently synonymized with *Pelomedusa subrufa* (Bonnaterre, 1789) and provide mitochondrial DNA sequences of type specimens or topotypic material for most taxa. Lectotypes are designated for *Testudo galeata* Schoepff, 1792, *Pentonyx capensis* Duméril & Bibron, 1835, *Pelomedusa nigra* Gray, 1863, *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910, and *Pelomedusa galeata damarensis* Hewitt, 1935. For *Pelomedusa gasconi* Rochebrune, 1884, a taxon without preserved type material, a neotype is designated. Type material of *Pentonyx americana* Cornalia, 1849, a nominal species without credible type locality, is lost and its identity remains questionable. Also the holotype of *Pelomedusa galeata orangensis* Hewitt, 1935 is lost, but its allocation to the only genetic lineage occurring in South Africa is unambiguous. Phylogenetic analyses of type sequences or topotypic material reveal that the remaining nominal taxa represent three of the nine previously identified lineages of *Pelomedusa*. Among these three lineages is the South African one. Type specimens of *Pentonyx gehafie* Rüppell, 1835 correspond to an additional distinct lineage. The present study provides a sound basis for a subsequent integrative taxonomic revision of the *Pelomedusa* complex.

Key words: Africa, Arabian Peninsula, Madagascar, nomenclature, type specimen

Introduction

Helmeted terrapins (*Pelomedusa subrufa*) are widely distributed over sub-Saharan Africa, Madagascar and the southwestern Arabian Peninsula (Iverson 1992; Ernst *et al.* 2000; Boycott & Bourquin 2008) and thought to represent an example of a pan-African reptile species (Wong *et al.* 2010; Barlow *et al.* 2013). With maximum shell lengths of 20–32.5 cm (Ernst *et al.* 2000), helmeted terrapins are a small to medium-sized species and adapted to a peculiar life style. These terrapins use small, often temporary water bodies. If these dry out, the terrapins burrow underground and remain there until more favourable conditions return. Moreover, the terrapins are able to move great distances overland, allowing them to occur in quite arid regions. Helmeted terrapins thus occupy a unique ecological niche among African freshwater turtles (Boycott & Bourquin 2008; Branch 2008).

Currently, *P. subrufa* is treated as monotypic (Gasperetti *et al.* 1993; Fritz & Havaš 2007; Boycott & Bourquin 2008; van Dijk *et al.* 2012), even though many previous authors recognized two or three distinct subspecies before Gasperetti *et al.* (1993) questioned the reliability of their diagnostic morphological characters. However, using mitochondrial and nuclear DNA sequences, two recent papers (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010) revealed deep genealogical lineages in *P. subrufa*, suggesting that *Pelomedusa* represents rather a species complex

(Vargas-Ramírez *et al.* 2010). This is supported by the finding that genetic divergences among *Pelomedusa* lineages equal or exceed those observed between the species of African hinged terrapins (*Pelusios*), the most closely related genus to *Pelomedusa* (Fritz *et al.* 2011).

Vargas-Ramírez *et al.* (2010) identified several priorities for future taxonomic work on *Pelomedusa*. Among these, the proper taxonomic allocation of the many scientific names erected for helmeted terrapins over the past two centuries is of paramount importance. To address this issue, here we provide a detailed discussion of the junior synonyms of *Testudo subrufa* Bonnaterre, 1789 and use, as far as possible, mitochondrial DNA sequences of historical type specimens or topotypic material for determining their relationships.

The present paper is a further contribution to disentangle the taxonomy of morphologically difficult chelonians using DNA sequences of historical type specimens (*cf.* Fritz *et al.* 2008; Präsag *et al.* 2008; Stuart & Fritz 2008; Stuckas & Fritz 2011; Stuckas *et al.* 2013).

Material and methods

Material and sampling. Historical type specimens representing the majority of taxa currently synonymized with *Pelomedusa subrufa* were examined (Tables 1, S1) and their straight carapacial lengths were taken to the nearest mm using a calliper. Small pieces of tissue were extracted from inside of most types (Tables 2, S1). In addition, one fresh tissue sample and one tissue sample from a museum specimen (Table S1) were studied to enrich the partly overlapping data sets of Vargas-Ramírez *et al.* (2010), Wong *et al.* (2010) and Fritz *et al.* (2011). Moreover, the fresh samples of Vargas-Ramírez *et al.* (2010) were used to generate sequences of the 12S rRNA gene (Table S1), if these were not available from Wong *et al.* (2010) and Fritz *et al.* (2011).

Chosen genetic markers and primer design. Three mtDNA fragments were chosen which are useful in discriminating the previously identified nine genetic lineages of *Pelomedusa* (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010), namely, part of the 12S ribosomal RNA gene (12S rRNA or 12S), the partial cytochrome *b* gene (*cyt b*), and part of the 3' half of the NADH dehydrogenase subunit 4 gene (ND4) plus adjacent DNA coding for tRNAs. For PCR and sequencing of fresh samples, established primer pairs were applied (Table S2). However, DNA from historical type and museum specimens is generally much degraded and fragmented. Therefore, new primers were designed for each marker gene using consensus sequences of all nine *Pelomedusa* lineages to generate short DNA fragments for reconstructing phylogenetically informative longer sequences. A first primer set yielding in part non-overlapping mtDNA fragments was based on this approach, and a second primer generation was then developed that specifically targets the obtained DNA fragments in order to bridge the gaps with overlapping sequences (Table S3).

DNA extraction, PCR and sequencing. Total genomic DNA of fresh samples was extracted using the innuPREP DNA Mini Kit (Analytik Jena AG, Jena, Germany). PCR was performed using 1–5 µl of DNA extraction in a 20 µl volume containing 0.5 µM of each primer, 0.5 mM of each dNTP (Fermentas, St. Leon-Rot, Germany), 1 unit of *Taq* polymerase (Bioron DFS-Taq, Bioron GmbH, Ludwigshafen, Germany), 2 µl PCR buffer 10× incl. MgCl₂, and ultrapure H₂O. Primers and PCR programs are summarized in Tables S2 and S4. PCR products were visualised on a 1% agarose gel. PCR products were cleaned up using the ExoSAP-IT reagent (USB Europe GmbH, Stauf, Germany; 1:20 dilution, modified protocol: 30 min at 37°C, 15 min at 80°C). If necessary, DNA bands were alternatively excised from a 2% agarose gel and purified using the peqGOLD Gel Extraction Kit (PEQLAB Biotechnologie GmbH, Erlangen, Germany). For cycle sequencing the same forward and reverse primers were used as for PCR (Table S2). The total reaction volume of 10 µl contained 2 µl sequencing buffer, 1 µl premix, 0.5 µM of the respective primer, 0.5–6 µl DNA template, and ultrapure H₂O. Using the ABI PRISM Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA), 25–30 cycles were performed at 96°C for 10 s, 50°C for 5 s and 60°C for 4 min. Reaction products were purified using Sephadex™ G-50 fine (GE Healthcare, München, Germany). Sequencing was performed on an ABI 3130xl Genetic Analyser (Applied Biosystems).

Extraction of historical material was carried out in a clean room, which is physically isolated from all other DNA processing facilities. Prior to this study, no *Pelomedusa* material had been studied there (fresh samples used in the present study, Vargas-Ramírez *et al.* 2010, and Fritz *et al.* 2011 were processed in the main laboratory, which is located in another building). All work in the clean room was performed in three different HERAsafe KSP 9

safety cabinets (Thermo Fisher Scientific, Waltham, MA, USA) corresponding to the working steps sample preparation, DNA extraction, and PCR setup. Safety cabinets and clean room were irradiated with UV light for at least 6 h before and after every working step. For DNA extraction, the sbeadex forensic kit (LGC Genomics, Berlin, Germany) was used according to the manufacturer's standard protocol. PCR setup was identical to fresh samples, except that 1 µl of Mg²⁺ and 0.2 µl (20 ng/µl) of Bovine Serum Albumin (Fermentas) were added to each sample. Primers and PCR programs used for historical samples are summarized in Tables S3 and S4. Thermocycling was carried out in the main laboratory, and a positive control (containing DNA of a fresh *Pelomedusa* sample, extracted with standard methods in the normal DNA processing facility) and a negative control (all reagents except the DNA template) were always processed downstream along with the historical samples. Additional working steps were identical as for fresh material. For the 12S rRNA gene, three mtDNA fragments of 92–124 bp (after primers were trimmed) yielded a total sequence length of 251–252 bp, dependent from the presence of a deletion. For the *cyt b* gene, six overlapping fragments of 63–115 bp resulted in a contig of 319 bp length, and for the ND4 gene, eight overlapping fragments of 75–122 bp yielded a final sequence length of 437 bp (*cf.* Tables S5–S7). However, only up to 435 bp of the ND4 gene could be read.

Alignment and phylogenetic analyses. Obtained DNA sequences were checked manually for base-calling errors and aligned in BIOEDIT 7.0.9.0 (Hall 1999). For calculations, the sequences of all three mtDNA fragments (12S, *cyt b*, ND4+tRNAs) were concatenated and merged with previously published homologous *Pelomedusa* sequences (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fritz *et al.* 2011), resulting in a total alignment of 76 *Pelomedusa* sequences and 1848 bp length. *Pelusios sinuatus* was added as outgroup (Table S1; see there for GenBank accession numbers).

Phylogenetic relationships were then inferred using Bayesian and Maximum Likelihood (ML) approaches and an alignment partitioned by gene (the short sequences coding for tRNAs corresponded only to one partition).

For Bayesian analyses, the best evolutionary model for each partition was determined in MRMODELTEST 2.3 (Nylander 2004) by the Akaike Information Criterion (Table S8). Calculations were performed with MRBAYES 3.2.1 (Ronquist *et al.* 2012) using two parallel runs (each with four chains) and default parameters. The chains ran for 10 million generations with every 100th generation sampled. The calculation parameters were analysed using a burn-in of 2.5 million generations to assure that both runs converged. Subsequently, only the plateau of the most likely trees was sampled using the same burn-in, and a 50% majority rule consensus tree was generated. The posterior probability of any individual clade in this consensus tree corresponds to the percentage of all trees containing that clade, and is a measure of clade frequency and credibility.

ML analyses were conducted using RAxML 7.2.8 (Stamatakis 2006) and the default GTR+G model. Five independent ML searches were run using different starting conditions and the fast bootstrap algorithm to explore the robustness of the branching patterns by comparing the best trees. Subsequently, 1000 non-parametric thorough bootstrap replicates were calculated and the values plotted against the best tree.

Results and discussion of nominal taxa and type specimens

Fritz & Havaš (2007) and van Dijk *et al.* (2012) list 14 species group names as subjective junior synonyms of *Testudo subrufa* Lacepède, 1788 = *Testudo subrufa* Bonnaterre, 1789. However, as is obvious from the original descriptions (Donndorff 1798: p. 34; Suckow 1798: p. 49), *Testudo badia* Donndorff, 1798 and *Testudo rubicunda* Suckow, 1798 represent merely replacement names (*nomina nova*) for *Testudo subrufa* and are therefore objective junior synonyms (ICZN 1999: Art. 72.7). Consequently, in addition to *Testudo subrufa*, 12 names remain which need to be considered (Table 1).

We succeeded in generating mitochondrial DNA sequences of type specimens or topotypic material for most of these nominal taxa (except *Pentonix americana* Cornalia, 1849 and *Pelomedusa galeata orangensis* Hewitt, 1935), allowing their identification with genetic lineages (Fig. 1; Table 2). Below we discuss each nominal taxon and its genetic assignment, repeat the original spellings of type localities and add, when necessary, in square brackets the current names of type localities or explanations.

TABLE 1. Nominal taxa currently identified with *Pelomedusa subrufa* (Bonnaterre, 1789) and their name-bearing type specimens. Museum acronyms: BMNH—The Natural History Museum, London; MNHN—Muséum National d'Histoire naturelle, Paris; NRM—Swedish Museum of Natural History, Stockholm; PEM—Port Elizabeth Museum; SMF—Senckenberg-Museum, Frankfurt am Main; ZFMK—Zoologisches Forschungsmuseum Alexander Koenig, Bonn; ZMUL—Biological Museum of Lund University.

Name	Original type locality	Name-bearing type(s)
<i>Testudo subrufa</i> Bonnaterre, 1789	Inde [India, in error]	Holotype: MNHN 7970
<i>Testudo galeata</i> Schoepff, 1792	India orientalis [East India, in error]	Originally syntypes: ZMUL 6481, one specimen catalogued as NRM 7043; lectotype (here designated): ZMUL 6481
<i>Emys olivacea</i> Schweigger, 1812	Nigritia [Senegal]	Holotype: MNHN 7971
<i>Pentonyx capensis</i> Duméril & Bibron, 1835	Cap de Bonne-Espérance, Madagascar, Sénégal [Cape of Good Hope, Madagascar, Senegal]	Originally syntypes: MNHN, all <i>Pelomedusa</i> specimens present at time of description; lectotype (here designated): MNHN 9506
<i>Pentonyx gelafie</i> Rüppell, 1835	Östlicher Abhang der abyssinischen Küstengebirge [eastern slope of coastal mountains, Eritrea]	Lectotype (Mertens 1937): SMF 7947
<i>Pentonyx americana</i> Cornalia, 1849	Novum Eboracum [New York, in error]	Holotype: Museo Civico di Storia Naturale di Milano, destroyed
<i>Pelomedusa nigra</i> Gray, 1863	Natal [South Africa]	Originally syntypes: BMNH 1849.1.30.27, 1862.12.4.4-5; lectotype (here designated): BMNH 1849.1.30.27
<i>Pelomedusa gasconi</i> Rochebrune, 1884	Dagana, Saïdé, lac de N'Guer, marigot des Maringouins [mosquito oxbows of N'Gor lake, Dakar, Senegal]	No type preserved (Loveridge 1941), neotype (here designated): ZFMK 17076
<i>Pelomedusa galeata</i> var. <i>disjuncta</i> Vaillant & Granddier, 1910	Abyssinia [eastern slope of coastal mountains, Eritrea], shore of Lake Abaya, Sidamo, Ethiopia	Originally syntypes: MNHN 7870, 9398, 1902.346; lectotype (here designated): MNHN 7870
<i>Pelomedusa galeata damarensis</i> Hewitt, 1935	Quickborn near Okahandja, South West Africa [Namibia]	Originally syntypes: PEM R14953-R14954; lectotype (here designated): PEM R14953
<i>Pelomedusa galeata devilliersi</i> Hewitt, 1935	Besondermeid, Steinkopf, Namaqualand, C.P. [Cape Province, now Northern Cape, South Africa]	Holotype: PEM R14962
<i>Pelomedusa galeata orangensis</i> Hewitt, 1935	Kimberley neighbourhood (?) [Northern Cape, South Africa]	Holotype: McGregor Museum, Kimberley, lost
<i>Pelomedusa subrufa wetsteini</i> Mertens, 1937	Majunga, West-Madagascar [Mahajanga, western Madagascar]	Holotype: SMF 7958

TABLE 2. *Pelomedusa* type specimens studied genetically. Lengths of successfully sequenced mtDNA fragments indicated. For GenBank accession numbers, see Table S1. The cyt *b* sequence of ZFMK 17076 was generated by Wong *et al.* (2010). For museum acronyms, see Table 1.

Specimen	Nominal taxon	Type status	Condition	12S	cyt <i>b</i>	ND4
MNHN 7970	<i>Testudo subrufa</i> Bonnaterre, 1789	Holotype	Dry, shell	Failed	Failed	Failed
MNHN 9506	<i>Pentonyx capensis</i> Duméril & Bibron, 1835	Lectotype (here designated)	Dry, mounted	233 bp	319 bp	435 bp
SMF 7947	<i>Pentonyx gehafie</i> Rüppell, 1835	Lectotype (Mertens 1937)	Ethanol-preserved	109 bp	Failed	Failed
SMF 7948	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Ethanol-preserved	252 bp	Failed	368 bp
SMF 7949	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Ethanol-preserved	Failed	Failed	Failed
SMF 7953	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Dry, shell	Failed	Failed	Failed
SMF 7960	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Ethanol-preserved	Failed	Failed	Failed
SMF 7961	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Ethanol-preserved	Failed	Failed	Failed
SMF 7962	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Ethanol-preserved	Failed	Failed	Failed
SMF 33054	<i>Pentonyx gehafie</i> Rüppell, 1835	Paralectotype	Dry, skeleton	252 bp	319 bp	435 bp
BMNH 1849.1.30.27	<i>Pelomedusa nigra</i> Gray, 1863	Lectotype (here designated)	Dry, mounted	251 bp	Failed	Failed
BMNH 1862.12.4.4	<i>Pelomedusa nigra</i> Gray, 1863	Paralectotype	Dry, mounted	251 bp	Failed	Failed
BMNH 1862.12.4.5	<i>Pelomedusa nigra</i> Gray, 1863	Paralectotype	Dry, mounted	251 bp	Failed	Failed
ZFMK 17076	<i>Pelomedusa gasconi</i> Rochebrune, 1884	Neotype (here designated)	Ethanol-preserved	252 bp	64 bp	Failed
PEM R14953	<i>Pelomedusa galeata damarensis</i> Hewitt, 1935	Lectotype (here designated)	Dry, shell	252 bp	Failed	Failed
PEM R14954	<i>Pelomedusa galeata damarensis</i> Hewitt, 1935	Paralectotype	Dry, shell	35 bp	319 bp	Failed
PEM R14962	<i>Pelomedusa galeata devilliersi</i> Hewitt, 1935	Holotype	Dry, shell	87 bp	100 bp	238 bp
PEM R9404	<i>Pelomedusa galeata orangensis</i> Hewitt, 1935	Paratype	Dry, shell	Failed	Failed	Failed
PEM R9408	<i>Pelomedusa galeata orangensis</i> Hewitt, 1935	Paratype	Dry, shell	Failed	Failed	Failed

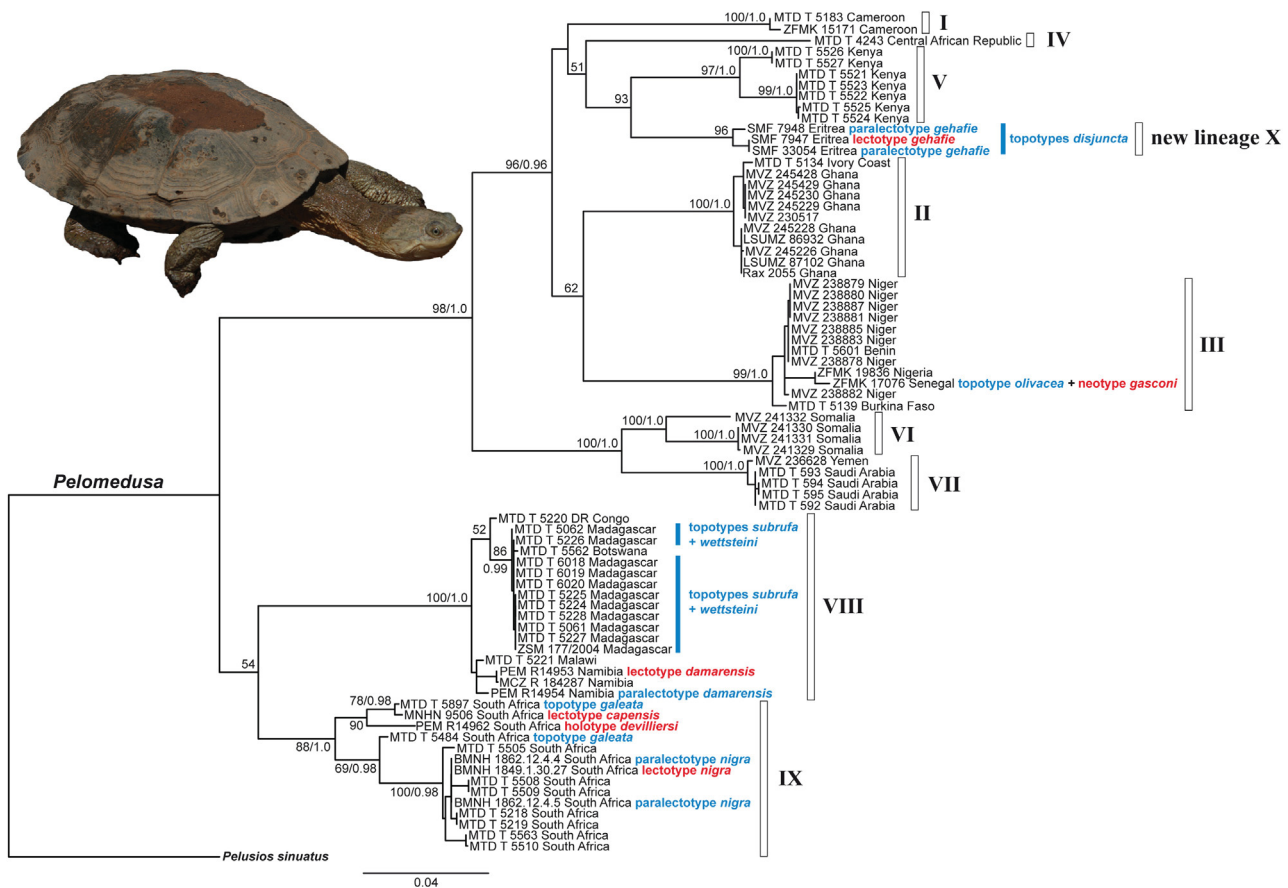


FIGURE 1. Maximum Likelihood tree for *Pelomedusa*, based on 1848 bp of mitochondrial DNA (12S, cyt *b*, ND4+tRNAs), rooted with *Pelusios sinuatus*. The tree topology completely matches the one inferred by Bayesian analyses. Numbers along nodes indicate bootstrap support and Bayesian posterior probabilities greater than 50 or 0.95, respectively (not shown for some terminal clades with short branches). Sample codes are voucher numbers; see Table S1 for explanation. Name-bearing types (red) and paralectotypes or topotypic samples (blue) highlighted. On the right, mitochondrial lineages of Vargas-Ramírez *et al.* (2010) indicated. No topotypic material of *Pelomedusa galeata orangensis* Hewitt, 1935 could be sequenced. However, the lost holotype is thought to come from the vicinity of Kimberley (South Africa) and all South African samples belong to lineage IX, so it can be concluded that *Pelomedusa galeata orangensis* represents the same lineage. Inset: Helmeted terrapin from the Addo Elephant National Park, South Africa. Photo: M. Gregorić.

Testudo subrufa Lacepède, 1788 = *Testudo subrufa* Bonnaterrre, 1789

Only when Mertens (1937: p. 139) and Loveridge (1941: p. 470) reinstated the scientific name *Pelomedusa subrufa* (Lacepède, 1788) for helmeted terrapins, this name combination found wide acceptance. Previously, *Pelomedusa galeata* (Schoepff, 1792) was used by most authors (see below under *Testudo galeata* Schoepff, 1792), even though John Edward Gray in his influential works consistently applied the species name *subrufa* (as *Hydraspis subrufa*, Gray 1831: p. 39 or *Pelomedusa subrufa*, e.g., Gray 1856: p. 53; 1863: pp. 99–100).

The name *Testudo subrufa* was originally coined by Lacepède (1788) in his “*Histoire Naturelle des Quadrupèdes Ovipares*”, where a specimen from the Royal Cabinet Paris was described under the name “*La Roussâtre*” (p. 173). In the “*Synopsis methodica Quadrupedum oviparorum*” of the same work, a folded table in which binomials were applied to the individual species, Lacepède named this terrapin *Testudo subrufa*. According to Lacepède (1788: p. 173) the terrapin on which he based his description was obtained from Pierre Sonnerat (1745–1814) and came allegedly from “Inde”.

This specimen, which has to be identified with the holotype of *Testudo subrufa* Lacepède, 1788, is still present in the collection of the Muséum National d’Histoire naturelle (Bour 1982) and was examined by us; tissue for genetic examination was extracted. The type (MNHN 7970) is a shell of an adult terrapin (straight carapacial length 13.67 cm) with most epidermal scutes missing. Its plastron is broken (Fig. 2).



FIGURE 2. Dorsal and ventral view of the holotype of *Testudo subrufa* Bonnaterre, 1789 (MNHN 7970, straight carapacial length 13.67 cm). Scale bar, 3 cm. Photos: M.D. Hofmeyr.

Since the International Commission on Zoological Nomenclature (ICZN 2005: Opinion 2104, Case 3226) has ruled that Lacepède's (1788) "*Histoire Naturelle des Quadrupèdes Ovipares*" is an unavailable non-binominal work, Bonnaterre (1789) became author of *Testudo subrufa* (and of other names) by re-publishing Lacepède's descriptions using consistently binominal scientific names. The type status of the terrapin described by Lacepède (1788) and re-described by Bonnaterre (1789: p. 28) remains unaffected by this transfer of formal authorship.

It is obvious that the original type locality ("Inde") of *Testudo subrufa* is in error. In accordance with the information provided by Lacepède (1788), Mertens (1937: p. 139) and Loveridge (1941: p. 470) believed that the type specimen of *Testudo subrufa* originates from Sonnerat, who is known to have collected at the Cape of Good Hope. Therefore, they identified the type locality with the Cape. However, based on an extensive discussion of historical details, Bour (1982) concluded that the holotype of *Testudo subrufa* was most probably not collected by Sonnerat, but by Philibert Commerson (1727–1773), who stayed on Madagascar in 1770. Some drawings of Commerson's Malagasy specimens are still present in the Central Library of the Paris Museum. Bour (1982) identified one of these drawings with the holotype and designated "Taolañaro (Fort-Dauphin), République Malagasy [Madagascar]" (p. 535) as type locality of *Testudo subrufa*. However, probably due to oversight, Bour (1985: p. 56) endorsed later the Cape of Good Hope as type locality of *Testudo subrufa* again.

All of our efforts to generate mtDNA sequences from the holotype resulted only in contaminant fungal sequences. Therefore, in the absence of other evidence, we accept the type locality Taolañaro (Madagascar), as suggested by Bour (1982). Consequently, the name *Testudo subrufa* Bonnaterre, 1789 refers to lineage VIII of Vargas-Ramírez *et al.* (2010), which is known to occur in Madagascar, Botswana, the Democratic Republic of the Congo, Malawi and Namibia (Fig. 1). The Malagasy populations are thought to be introduced from continental Africa (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010). If lineage VIII is deemed to be taxonomically distinct, the name *Pelomedusa subrufa* (Bonnaterre, 1789) will have to be restricted to this taxon.

***Testudo galeata* Schoepff, 1792**

The name *Testudo galeata* was erected by Schoepff (1792: p. 12) in his famous "*Historia Testudinum iconibus illustrata*". For a long time *Testudo galeata* was used for helmeted terrapins, until Mertens (1937) and Loveridge

(1941) pointed out that the older name *Testudo subrufa* should be applied. Schoepff's original description was based on detailed unpublished notes received from two Swedish naturalists. Originally, Schoepff (1792: pp. 12–16) intended to assemble information about another terrapin species, *Testudo scabra* Linnaeus, 1758, a taxon whose identity puzzled scientists for about 250 years (Rhodin & Carr 2009).

Schoepff received from Anders Jahan Retzius (1742–1821) of Lund a detailed description and drawings of a “*Testudo scabra*” from “India orientalis” [East India], which Retzius had kept alive for two years. Schoepff (1792) published Retzius' description (pp. 13–14) and a coloured etching of the terrapin as figure 1 in plate III. Shown under the name “*Test. scabra* Retz.”, it is clearly a juvenile *Pelomedusa subrufa* (Fig. 3, top), and “Prof. D. Swartz” (probably to be identified with Olof Peter Swartz, 1760–1818) of Stockholm wrote to Schoepff that a very similar specimen in spirit is present in the Cabinet of the Royal Academy of Sciences at Stockholm. Schoepff (1792: p. 16) concluded that these two terrapins could represent a new species, for which he proposed the name *Testudo galeata*. The eponymous character (*galeata*, Latin = helmeted) of this putative new species is its helmet-like head scalation. The two terrapins from Lund and Stockholm have to be regarded as syntypes of *Testudo galeata*.

In the collection of the Biological Museum of Lund University there is still extant a single alcohol-preserved *Pelomedusa* specimen, bearing the catalogue number ZMUL 6481 (Fig. 3, bottom). Retzius donated this terrapin as “*Testudo scabra*” in 1811 to the Lund Museum, together with a large collection of other specimens (L. Lundqvist, pers. comm.). We conclude that ZMUL 6481, which originates evidently from Retzius, has to be identified with the syntype described in detail in Schoepff (1792: pp. 13–14). The size of ZMUL 6481 (straight carapacial length 5.84 cm, width 4.97 cm) approximately matches the measurements given in Schoepff (1792: p. 13) with 2 ½ and 2 Prussian inches (1 Prussian inch = 2.615 cm), especially when it is considered that Retzius could have measured over the curve of the carapace. However, the shell shape of ZMUL 6481 is a bit too oval compared to Schoepff's figure (Fig. 3, top). Retzius' two original drawings of the terrapin and part of his letter have survived among Schoepff's legacy, and are now kept in the Museum für Naturkunde, Berlin (Fig. 3, top). The original drawings are very rough, but they illustrate a shell shape that agrees better with ZMUL 6481 than with Schoepff's (1792) published figure. In comparison it appears that Schoepff's figure is somewhat idealized. The coloration of the syntype is much faded due to the age of the specimen and allows no direct comparison with the description in Schoepff (1792).

In the Swedish Museum of Natural History, Stockholm, there are two old *Pelomedusa* specimens catalogued as one lot (NRM 7043), which were once part of the collection of Charles de Geer (1720–1778). These specimens were transferred by his widow to the collection of the Royal Swedish Academy of Sciences in 1778. The two alcohol-preserved terrapins are in quite bad condition with many shell scutes missing. They are the only helmeted terrapins which were present in the collection when Swartz corresponded with Schoepff, so that one of these specimens is most likely the second syntype (E. Åhlander, pers. comm.). However, as it cannot be unambiguously identified, we choose to designate hereby the Lund specimen as lectotype of *Testudo galeata* Schoepff, 1792.

Hewitt (1935: p. 326) corrected the type locality “India orientalis” of *Testudo galeata* to the environs of Cape Town (and not Cape Flats as thought by Mertens 1937: p. 139, later repeated by Loveridge 1941: p. 470). This makes sense as the Dutch East India Company (Vereenigde Oost-Indische Compagnie) in 1652 established an outpost near the Cape of Good Hope for provisioning their ships coming from East India. This outpost, later becoming the Cape Colony and finally Cape Town, was a supplier of early natural history specimens for Europe (Wren-Sargent 1999; Bauer & Günther 2013; Bauer & Wahlgren 2013), and such specimens might have been mixed up or confused with materials coming from East India. Gray (1831: p. 40) wrote exactly in this spirit about helmeted terrapins “I have never seen this tortoise from India, but being brought from the Cape by the Indian ships, they, as well as many other Cape animals, are often called Indian.” Also the morphology of the Lund type, which has pectoral scutes in broad midline contact, is typical for South African terrapins (Hewitt 1935: p. 325; unpubl. observ.), and is thus in agreement with an origin near Cape Town. Therefore, we accept Hewitt's type locality designation and identify *Testudo galeata* with *Pelomedusa* lineage IX, distributed throughout South Africa (Vargas-Ramírez *et al.* 2010).

Two fresh *Pelomedusa* samples collected close to the Cape of Good Hope (MTD T 5484, Swellendam District; MTD T 5897, Chelance; Table S1) can be regarded as topotypes of *Testudo galeata*. As expected, their DNA sequences (Vargas-Ramírez *et al.* 2010; this study) are assigned with high support to lineage IX in phylogenetic analyses (Fig. 1).



FIGURE 3. Top, left: Folio from Schoepff's legacy (Museum für Naturkunde zu Berlin, Historische Bild- und Schriftgutsammlungen, SI, Nachl. Schoepff II) consisting of the drawings provided by Retzius and an imprint of the resultant etching. Retzius' hand-written German text reads:

“Die Skizze der *T. scabra* welche ein Student gemacht hat, lege ich so fehlerhaft sie auch ist bey, indess aus Nr. 1 forma scutellorum u. aus Nr. 2 die Gestalt des Kopfes und der Hinterfüße wohl zu ersehen ist. Daß meine *Testudo* die wahre *scabra* L. ist, deßen bin ich gewiß, ob er [meant is Linnaeus] gleich sagt [illegible] er hat aber ganz gewiß Nr. 73 u. 74 [illegible] completirt, wie das oft der Fall ist.—Retzius” [sic].

English translation: “I enclose the drawing of the *T. scabra* made by a student, as flawed as it is, since no. 1 shows well the shape of the scutes and no. 2 the shape of the head and of the hind legs. I am sure that my *Testudo* is the true *scabra* L., even though he [meant is Linnaeus] says [illegible] he has surely no. 73 and 74 [illegible] completed, as this is often the case.—Retzius” [sic].

Top, right: reproduction of figure 1, plate III from Schoepff (1792) showing “*Test. scabra* Retz.”.

Bottom: Dorsal and ventral view of the lectotype of *Testudo galeata* Schoepff, 1792 (ZMUL 6481, straight carapacial length 5.84 cm). Scale bar, 3 cm. Photos: L. Lundqvist.

***Emys olivacea* Schweigger, 1812**

Schweigger (1812: p. 307) described a carapace from the Adanson Collection of the Paris Museum as the new species *Emys olivacea*. According to the original description, the specimen originates “in sabulosis Nigritiae” [in the sands of Senegal] and is still present in the collection of the Muséum National d'Histoire naturelle, Paris (MNHN 7971). This specimen was not available to us.

Starting with Loveridge (1941), many authors used the name *Pelomedusa subrufa olivacea* for helmeted terrapins from the more northern parts of the species' range, which usually have the pectoral scutes of the plastron separated, even though this character cannot be determined in the holotype, which consists only of a carapace. Moreover, Gasperetti *et al.* (1993) disputed the reliability of this trait, and since then most authors have treated *P. subrufa* as monotypic (see above and the review in Boycott & Bourquin 2008).

In our phylogenetic analyses (Fig. 1), the concatenated 12S and *cyt b* sequences (Wong *et al.* 2010; this study) of a Senegalese *Pelomedusa* (ZFMK 17076) are assigned with high support to lineage III of Vargas-Ramírez *et al.* (2010). The placement of this topotypic terrapin suggests that *Emys olivacea* has to be identified with lineage III, which is otherwise known to occur in Benin, Burkina Faso, Niger, and Nigeria (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010). The pectoral scutes of ZFMK 17076 are triangular, but the tips just meet in the midline of the plastron. A comparison of 21 helmeted terrapins from Niger, Nigeria, and Senegal from the collections of the natural history museums in Bonn, Frankfurt am Main, London, Port Elizabeth, and Vienna shows that specimens with pectoral scutes in narrow contact, as well as specimens with completely separated pectorals, both occur in lineage III.

If terrapins of lineage III should be regarded as taxonomically distinct in the future, *Emys olivacea* Schweigger, 1812 would be the oldest available name.

***Pentonyx capensis* Duméril & Bibron, 1835**

Based on all *Pelomedusa* specimens present in the collection of the Paris Museum upon the time of the species description, Duméril & Bibron (1835: pp. 390–394) erected *Pentonyx capensis*. The series of syntypes comprised helmeted terrapins from the eponymous South African Cape Region and from Madagascar, but also the holotype of *Emys olivacea* from Senegal, which was considered by Duméril & Bibron to represent merely a juvenile *Pentonyx capensis*. We examined one of the syntypes, MNHN 9506 originating from “Le Cap”, and were allowed to extract tissue for genetic investigation. MNHN 9506 is an adult mounted male in good condition with a straight carapacial length of 23.45 cm (Fig. 4).

Mertens (1937: p. 139) restricted the type locality of *Pentonyx capensis* to the Cape of Good Hope. However, because no lectotype was designated this action was invalid (*cf.* ICZN 1999: Art. 76). Nevertheless, later authors identified *Pentonyx capensis* implicitly or explicitly with the nominotypical subspecies of the helmeted terrapin, if the species was treated as polytypic (Mertens 1937; Loveridge 1941; Bour 1986; Ernst & Barbour 1989; Iverson 1992). To stabilize this usage, we designate herewith MNHN 9506 as lectotype of *Pentonyx capensis*.

For the lectotype, mtDNA fragments of all three marker genes could be sequenced (Table 2). In phylogenetic analyses (Fig. 1), the concatenated sequences of MNHN 9506 are embedded within other South African sequences representing lineage IX *sensu* Vargas-Ramírez *et al.* (2010). Thus, if lineage IX should be deemed taxonomically distinct, *Pentonyx capensis* Duméril & Bibron, 1835 would become a subjective junior synonym of *Testudo galeata* Schoepff, 1792.

***Pentonyx gehafie* Rüppell, 1835**

Rüppell (1835: pp. 2–3) described *Pentonyx gehafie* based on terrapins which he found “häufig in allen fliessenden oder stagnirenden Gewässern auf dem östlichen Abhänge der abyssinischen Küstengebirge” [frequently in all flowing and stagnant waters on the eastern slope of the Abyssinian coastal mountains]. Rüppell diagnosed *Pentonyx gehafie* from the *Pentonyx* species occurring at the Cape of Good Hope by the plastral scutation: The pectoral scutes of his new species are triangular and do not reach the median plastral seam, whereas in the Cape species the pectoral scutes are in contact. The character state of the Abyssinian specimens is nicely depicted in

Rüppell's plate 1. Obviously Rüppell collected quite a number of helmeted terrapins, which originally had all syntype status. Mertens (1937: p. 140) mentions that seven of these specimens are in the Senckenberg Museum, Frankfurt am Main. However, there are eight, and not seven, terrapins collected by Rüppell with identical data (SMF 7947–7949, SMF 7953, SMF 7960–7962, SMF 33054). Whilst SMF 7947–7949 and SMF 7960–7962 are alcohol-preserved, SMF 7953 and SMF 33054 are dry specimens (Table 2). SMF 7947 was designated by Mertens (1937: p. 140) as lectotype, which is why the remaining terrapins bear today the status of paralectotypes. Further paralectotypes collected by Rüppell are in the Natural History Museum, London (Gray 1856: p. 53; Boulenger 1889: p. 199) and the Muséum National d'Histoire naturelle, Paris (see below under *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910). The lectotype is a subadult female of 11.42 cm straight carapacial length (Fig. 5, top).



FIGURE 4. Dorsal and ventral view of the lectotype of *Pentonyx capensis* Duméril & Bibron, 1835 (MNHN 9506, male, straight carapacial length 23.45 cm). Scale bar, 3 cm. Photos: M.D. Hofmeyr.

Mertens (1937: p. 140) restricted the type locality of *Pentonyx gehafie* to “Massaua” [also known as Massawa, Missiwa or Mitsiwa, Eritrea], a town within the source region of the type specimens. However, according to Article 76.1 of the International Code of Zoological Nomenclature (ICZN 1999), the type locality “is the geographical [...] place of capture, collection or observation of the name-bearing type.” Thus, Rüppell's original type locality has to remain unchanged and is to be identified with the eastern slope of coastal mountains, Eritrea.



FIGURE 5. Dorsal and ventral views of the lectotype of *Pentonyx gehafie* Rüppell, 1835 (SMF 7947, subadult female, straight carapacial length 11.42 cm; top) and of one of the paralectotypes in the Natural History Museum, London (BMNH 1947.3.5.78, adult male, straight carapacial length 16.70 cm; bottom). Scale bars, 3 cm. Photos: E. Morawa, P. Campbell.

Boulenger (1880: p. 151) synonymized *Pelomedusa gehafie* with *Pelomedusa galeata* (= *Pelomedusa subrufa*) because he studied specimens with intermediate plastral characters from Madagascar, the Upper Nile Region, and Zanzibar, even though he acknowledged that separated triangular pectorals never occur in South African terrapins and that in Abyssinia the terrapins have consistently widely separated triangular pectorals. Based on similar observations, but drawing a completely different conclusion, Hewitt (1935: p. 325) recognized “*Pelomedusa gehafiae*” [sic] as a valid species and opposed it to his polytypic species *Pelomedusa galeata*. Hewitt noted that at Mt. Elgon (border region of Uganda and Kenya) helmeted terrapins with separated pectorals are found together with terrapins having the pectorals in contact. Finally, based on the occurrence of morphologically intermediate terrapins in some regions, Parker (1936: p. 609) and Mertens (1937: p. 140) recognized *Pentonyx gehafie* as a valid subspecies of the helmeted terrapin and used the names *Pelomedusa galeata gehafie* and *Pelomedusa subrufa gehafie*, respectively. In a similar vein, Loveridge (1941: p. 480) accepted the validity of a subspecies characterized by separated triangular pectoral scutes, but placed *Pentonyx gehafie* in the synonymy of *Pelomedusa subrufa olivacea* (Schweigger, 1812). Summarizing his own observations and those of previous authors, Loveridge believed that this taxon occurs in “the drier regions of a belt extending from Senegal to Eritrea, intergrading with the typical form in the Anglo-Egyptian Sudan, Ethiopia, Somaliland, northern Kenya and Uganda” (p. 481). Later authors identified *Pelomedusa subrufa olivacea* generally with the more northern populations of the helmeted terrapin, including the populations of the Arabian Peninsula (cf. Ernst & Barbour 1989; Iverson 1992; Ernst *et al.* 2000; Boycott & Bourquin 2008), until the usage of subspecies was abandoned after Gasperetti *et al.* (1993).

For the present investigation, we studied the lectotype and the nine paralectotypes of *Pentonyx gehafie* in Frankfurt am Main and London; all specimens conform well to the description by Rüppell (1835) in having widely separated triangular pectoral scutes (Fig. 5). Tissue for genetic examination was extracted from the eight Frankfurt specimens, but DNA sequences could be generated only for three terrapins, among them the lectotype (Table 2).

In phylogenetic analyses (Fig. 1), the sequences of the type specimens constitute a deeply divergent clade being sister to Kenyan terrapins representing lineage V *sensu* Vargas-Ramírez *et al.* (2010). We examined 18 *Pelomedusa* from Kenya morphologically (7 live terrapins and 11 specimens in the collections of the natural history museums of Berlin, Bonn, London, and Vienna) and these differ consistently from the type series of *Pentonyx gehafie* in that their pectoral scutes are in wide contact in the midline, suggesting that *Pentonyx gehafie* could be a distinct taxon. At present, we refer to the genetic lineage of the type specimens of *Pentonyx gehafie* as lineage X, and do not relate it to any of the lineages identified by Vargas-Ramírez *et al.* (2010).

***Pentonix* [sic] *americana* Cornalia, 1849**

Cornalia (1849: pp. 312–313) described a specimen allegedly from “Novæboracum” [= Novum Eboracum, New York] under this name. After its description, *Pentonix americana* has never been regarded as a valid taxon. It is traditionally identified with the helmeted terrapin (e.g., Boulenger 1889: p. 198; Mertens 1937: p. 139; Loveridge 1941: p. 473; Wermuth & Mertens 1961: p. 284, 1977: p. 115; Fritz & Havaš 2007: p. 345; van Dijk *et al.* 2012: p. 000.295), even though Strauch (1865: p. 111) doubted that it could be reliably assigned to any species. The type specimen was in the collection of the natural history museum of Milan (Museo Civico di Storia Naturale di Milano) and was destroyed, together with most of the herpetological collection, by British air raids in 1943 (S. Scali, pers. comm.).

Pentonix americana is best treated as *nomen dubium*, because there is no further information available. Mertens’ (1937: p. 139) identification of “*Pentonyx americana*” with South African helmeted terrapins (“offenbar ein südafrikanisches Stück”), and thus with the nominotypical subspecies *sensu* Mertens (1937), is pure speculation. Mertens’ suggestion was later repeated by Loveridge (1941: p. 473 “probably a South African specimen”).

***Pelomedusa nigra* Gray, 1863**

Based on three syntypes from Natal, Gray (1863) described the new species *Pelomedusa nigra*. Boulenger (1889) lists these specimens as *k*, *l* and *m* in his “*Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles of the British Museum (Natural History)*”. Today, these mounted dry specimens are catalogued under the numbers

BMNH 1849.1.30.27 and BMNH 1862.12.4.4–5 (the latter re-registered as BMNH 1947.3.5.80–81). *Pelomedusa nigra* was soon synonymized with *Pelomedusa galeata* (Strauch 1865: p. 111; Boulenger 1880: p. 151, 1889: p. 198) or *Pelomedusa subrufa* (Mertens 1937: p. 139; Loveridge 1941: p. 474), until Bour (1986: p. 37) resurrected it in a footnote as a subspecies of *Pelomedusa subrufa*. However, following Gasperetti *et al.* (1993) most authors abandoned the usage of any subspecies of *Pelomedusa subrufa* (*cf.* Boycott & Bourquin 2008).

The three syntypes of *Pelomedusa nigra* were examined for the present study and tissue for genetic investigation was extracted. We designate hereby the oldest specimen, BMNH 1849.1.30.27 (adult male, straight carapacial length 16.19 cm; Fig. 6, top), as lectotype of this taxon.

A fragment of the 12S rRNA gene could be sequenced from all three type specimens. In phylogenetic analyses (Fig. 1), these sequences cluster with high support within lineage IX from South Africa. Moreover, the three type sequences are identical with a 12S sequence of a fresh sample from the same geographical source region (MTD T 5509, Ndumo, KwaZulu-Natal). Since we identify *Testudo galeata* Schoepff, 1792 with lineage IX, *Pelomedusa nigra* Gray, 1863 would become a subjective junior synonym of that name, if lineage IX should be considered taxonomically distinct.

***Pelomedusa gasconi* Rochebrune, 1884**

Rochebrune (1884: pp. 25–26; plate 1: figs 1–2) described helmeted terrapins from several sites in Senegal (“Dagana, Saidé, lac de N’Guer, marigot des Maringouins” [the latter meaning mosquito oxbows of N’Gor lake, Dakar, Senegal]) as his new species *Pelomedusa gasconi*, which was later synonymized by Loveridge (1941: p. 480) with *Pelomedusa subrufa olivacea*. In accordance with this assignment, Rochebrune’s (1884) plate 1 shows a helmeted terrapin with widely separated pectoral scutes, although Rochebrune explained that this character may be variable (pp. 26–27). According to Angel (in Loveridge 1941: p. 480), there was no type specimen of *Pelomedusa gasconi* preserved. Loveridge (1941: p. 480) restricted the type locality to Dagana, Senegal, which is invalid without lectotype or neotype designation (*cf.* ICZN 1999: Art. 76).

The sites of the composed type locality are up to 400 km distant from one another. To restrict the type locality and to associate the name *Pelomedusa gasconi* Rochebrune, 1884 unambiguously with a genetic lineage of *Pelomedusa*, we designate in accordance with Article 75 (ICZN 1999) a topotypic specimen from Dakar as its neotype (ZFMK 17076, a subadult female of 11.18 cm straight carapacial length in alcohol; Fig. 6, bottom). For the neotype, mtDNA sequences are available (see also above under *Emys olivacea* Schweigger, 1812). Thus, the name *Pelomedusa gasconi* is to be identified with the same genetic lineage as *Emys olivacea* (lineage III of Vargas-Ramírez *et al.* 2010; Fig. 1) and becomes a subjective junior synonym of the latter name, if lineage III is deemed taxonomically distinct.

***Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910**

This taxon was treated by Loveridge (1941: p. 480) as a junior synonym of *Pelomedusa subrufa olivacea*. It was originally described by Vaillant & Grandidier (1910: pp. 55–56) as a new variety. These authors compared helmeted terrapins from Madagascar and the Cape of Good Hope with specimens of “*Pentonyx gehafie*” from the collection of the Muséum National d’Histoire naturelle, highlighting that the latter differ from Malagasy and South African individuals by separated pectoral scutes. Vaillant & Grandidier (1910: p. 56) assigned the terrapins with the separated pectorals to their new variety *Pelomedusa galeata* var. *disjuncta* and mention *expressis verbis* that specimens of Rüppell’s “*Pentonyx gehafie*” fitting this character are present in the holdings of the Paris Museum. Consequently, it is clear that the description of *Pelomedusa galeata* var. *disjuncta* was based on several syntypes. In addition to Rüppell’s specimens, Vaillant & Grandidier (1910: p. 56) mention another terrapin collected by Vicomte Pierre Marie Robert Du Bourg de Bozas (1871–1902) as representing their new variety. Based on this information and locality data from the Paris Museum provided by Fernand Angel, Loveridge (1941: p. 480) restricted the type locality of *Pelomedusa galeata* var. *disjuncta* to the “shore of Lake Abaya, Sidamo, Ethiopia”, where the specimen of Du Bourg de Bozas had been collected. However, this type locality restriction is invalid without lectotype designation (*cf.* ICZN 1999: Art. 76). The specimen in question is still present in the collection of

the Muséum National d'Histoire naturelle (MNHN 1902.346, “Bord du lac Abbay, Sidamo, Ethiopie”). In addition, there are also two specimens labelled as syntypes¹ of *Pentonyx gehafie* (MNHN 7870, 9398, “Abyssinie”), which bear also syntype status for *Pelomedusa galeata* var. *disjuncta*. Consequently, the latter taxon was based on three syntypes and the type locality encompasses distinct localities, the shore of Lake Abaya, Sidamo, Ethiopia, and Abyssinia. Abyssinia can be more exactly identified with the eastern slope of the coastal mountains in present-day Eritrea, where Rüppell (1835: p. 3) discovered his specimens (see also above under *Pentonyx gehafie* Rüppell, 1835).

The syntypes of *Pelomedusa galeata* var. *disjuncta* were not available for study. However, since mtDNA sequences could be produced for other type specimens of *Pentonyx gehafie* (see above), the identity of terrapins from the coastal mountain region of Eritrea could be clarified genetically. Therefore, we designate hereby the topotypic specimen MNHN 7870 from “Abyssinie”, being simultaneously a paralectotype of *Pentonyx gehafie* Rüppell, 1835, as lectotype of *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910. By this action, we associate the latter name unambiguously with a defined genetic lineage of *Pelomedusa*. Thus, if the distinct genetic lineage matching the name-bearing types of *Pentonyx gehafie* and *Pelomedusa galeata* var. *disjuncta* should be deemed taxonomically distinct, the latter name would be automatically a subjective junior synonym of *Pentonyx gehafie*.

***Pelomedusa galeata damarensis* Hewitt, 1935**

This subspecies was based on two syntypes (shells) from “Quickborn, near Okahandja, South West Africa” [Namibia] (Hewitt 1935: p. 338). Actually, Quickborn is a farm approximately halfway between Okahandja and Otjiwarongo, Namibia. Following Mertens (1937: p. 139) and Loveridge (1941: p. 474), *Pelomedusa galeata damarensis* was later synonymized with the nominotypical subspecies of the helmeted terrapin, if the species was regarded as polytypic. Herrmann & Branch (2013: p. 102) suggested that *Pelomedusa galeata damarensis* is morphologically distinctive and may deserve specific recognition.

The two syntypes of *Pelomedusa galeata damarensis* are now in the collection of the Port Elizabeth Museum (PEM R14953–R14954) and were examined for the present study. Whilst PEM R14953 is perfectly preserved, parts of the epidermal scutes on the right carapacial margin of PEM R14954 are missing. We designate herewith the better preserved specimen PEM R14953 (Fig. 7, top) as lectotype of *Pelomedusa galeata damarensis*. Tissue for genetic investigation was extracted from both type specimens. From PEM R14953, 252 bp of the 12S rRNA gene could be successfully sequenced, whereas only 35 bp of the 12S rRNA gene and 319 bp of the *cyt b* gene could be generated for PEM R14954 (Table 2).

In phylogenetic analyses (Fig. 1), the sequences of both type specimens are embedded with high support within lineage VIII of Vargas-Ramírez *et al.* (2010). The oldest available name for lineage VIII is *Testudo subrufa* Bonnatere, 1789 (see above), rendering *Pelomedusa galeata damarensis* Hewitt, 1935 a subjective junior synonym of the previous name, if lineage VIII should be regarded as taxonomically distinct.

***Pelomedusa galeata devilliersi* Hewitt, 1935**

The description of this subspecies was based on a single shell from “Besondermeid, Steinkopf, Namaqualand, C.P.” [Cape Province, now Northern Cape, South Africa] (Hewitt 1935: p. 337). Following Mertens (1937: p. 139) and Loveridge (1941: p. 474), *Pelomedusa galeata devilliersi* was later synonymized with the nominotypical subspecies of the helmeted terrapin, if the species was regarded as polytypic.

The holotype of *Pelomedusa galeata devilliersi* is now in the collection of the Port Elizabeth Museum (PEM R14962) and was examined for this study (Fig. 7, bottom). Tissue for genetic investigation was extracted and mtDNA fragments of all three marker genes could be sequenced (Table 2). In phylogenetic analyses (Fig. 1), the concatenated sequences are associated with high support with other South African samples representing lineage IX *sensu* Vargas-Ramírez *et al.* (2010), and thus *Pelomedusa galeata devilliersi* Hewitt, 1935 would become a junior synonym of *Testudo galeata* Schoepff, 1792, if lineage IX should be regarded as taxonomically distinct.

1. By lectotype designation of Mertens (1937) now paralectotypes, see above under *Pentonyx gehafie* Rüppell, 1835



FIGURE 6. Dorsal and ventral views of the lectotype of *Pelomedusa nigra* Gray, 1863 (BMNH 1849.1.30.27, adult male, straight carapacial length 16.19 cm; top) and of the neotype of *Pelomedusa gasconi* Rochebrune, 1884 (ZFMK 17076, subadult female, straight carapacial length 11.18 cm; bottom). Scale bars, 3 cm. Photos: P. Campbell, A. Petzold.



FIGURE 7. Dorsal and ventral views of the lectotype of *Pelomedusa galeata damarensis* Hewitt, 1935 (PEM R14953, adult male, straight carapacial length 14.0 cm; top) and of the holotype of *Pelomedusa galeata devilliersi* Hewitt, 1935 (PEM R14962, adult female, straight carapacial length 19.24 cm; bottom). Scale bars, 3 cm. Photos: W.R. Branch.



FIGURE 8. Dorsal and ventral view of the holotype of *Pelomedusa subrufa wettsteini* Mertens, 1937 (SMF 7958, adult male, straight carapacial length 12.26 cm). Scale bar, 3 cm. Photos: E. Morawa.

***Pelomedusa galeata orangensis* Hewitt, 1935**

Hewitt (1935: pp. 332–335) based the description of his new subspecies *Pelomedusa galeata orangensis* on several specimens from distinct collecting sites in South Africa. However, on page 333 he explicitly named a male shown in his plate XXXII, fig. 4, “the type”, so that it is clear that this specimen represents in accordance with Article 73.1 of the International Code of Zoological Nomenclature (ICZN 1999) the holotype of *Pelomedusa galeata orangensis*. This terrapin was in the Kimberley Museum (now McGregor Museum, Kimberley) and originates “presumably from the Kimberley neighbourhood” (Hewitt 1935: p. 333). Following Mertens (1937: p. 139) and Loveridge (1941: p. 474), *Pelomedusa galeata orangensis* was later synonymized with the nominotypical subspecies of the helmeted terrapin, if the species was regarded as polytypic.

The holotype of *Pelomedusa galeata orangensis* could not be located in the McGregor Museum (B. Wilson, pers. comm.), and must be considered lost. Efforts to sequence mtDNA of two paratypes from the collection of the Port Elizabeth Museum (PEM R9404, Warrenton, Northern Cape; PEM R9408, Thaba ‘Nchu, Free State) failed. However, genetic data were available for several South African localities encircling the type locality Kimberley (Vargas-Ramírez *et al.* 2010; this study), and all South African sequences correspond to lineage IX *sensu* Vargas-Ramírez *et al.* (2010). Consequently, we identify *Pelomedusa galeata orangensis* with this lineage. If lineage IX should be deemed taxonomically distinct, *Pelomedusa galeata orangensis* Hewitt, 1935 becomes a subjective junior synonym of *Testudo galeata* Schoepff, 1792.

Pelomedusa subrufa wettsteini Mertens, 1937

Based on five Malagasy specimens in the collection of the Senckenberg Museum, Mertens (1937: p. 141) described the subspecies *Pelomedusa subrufa wettsteini*. The holotype (SMF 7958) is an alcohol-preserved male from “Majunga, West-Madagascar” [Mahajanga, western Madagascar] with a straight carapacial length of 12.26 cm (Fig. 8). The taxon was soon synonymized with the nominotypical subspecies of the helmeted terrapin (Loveridge 1941: p. 474).

The type specimens were examined for this study, but tissue was not extracted because many DNA sequence data are available for Malagasy *Pelomedusa* (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fig. 1), which represent lineage VIII *sensu* Vargas-Ramírez *et al.* (2010). Thus, *Pelomedusa subrufa wettsteini* Mertens, 1937 would become a subjective junior synonym of *Testudo subrufa* Bonnaterre, 1789, if lineage VIII should be considered taxonomically distinct.

Conclusions

All previously named taxa of *Pelomedusa*, except *Pentonyx gehafie* Rüppell, 1835 and the doubtful *Pentonix americana* Cornalia, 1849, could be assigned to the nine mitochondrial lineages as defined by Vargas-Ramírez *et al.* (2010). *Pentonyx gehafie* Rüppell, 1835 represents a tenth distinct lineage (Fig. 1). Only four out of the ten genetic lineages are covered by existing names (Table 3). The oldest available name for lineage III *sensu* Vargas-Ramírez *et al.* (2010) is *Emys olivacea* Schweigger, 1812, with *Pelomedusa gasconi* Rochebrune, 1884 as its subjective junior synonym, if lineage III should be deemed taxonomically distinct. *Testudo subrufa* Bonnaterre, 1789 would have to be restricted to lineage VIII *sensu* Vargas-Ramírez *et al.* (2010), with *Pelomedusa galeata damarensis* Hewitt, 1935 and *Pelomedusa subrufa wettsteini* Mertens, 1937 as subjective junior synonyms. *Testudo badia* Donndorff, 1798 and *Testudo rubicunda* Suckow, 1798 are replacement names (*nomina nova*) for *Testudo subrufa* and, therefore, objective junior synonyms of this name. *Testudo galeata* Schoepff, 1792 would be the oldest available name for lineage IX *sensu* Vargas-Ramírez *et al.* (2010), with *Pentonyx capensis* Duméril & Bibron, 1835, *Pelomedusa nigra* Gray, 1863, *Pelomedusa galeata devilliersi* Hewitt, 1935, and *Pelomedusa galeata orangensis* Hewitt, 1935 as subjective junior synonyms. The oldest available name for the newly identified lineage X is *Pentonyx gehafie* Rüppell, 1835, with *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910 as subjective junior synonym. Thus, if the ten lineages should be considered taxonomically distinct, six *Pelomedusa* taxa were yet to be named. With the identification of the genetic allocation of the nominal taxa currently synonymized with *Pelomedusa subrufa* (Bonnaterre, 1789), the present study provides a sound basis for an integrative taxonomic revision of the *Pelomedusa* complex.

TABLE 3. Agreement between nominal taxa currently identified with *Pelomedusa subrufa* (Bonnaterre, 1789) and mitochondrial lineages.

Nominal taxon	mtDNA lineage
<i>Testudo subrufa</i> Bonnaterre, 1789	VIII
<i>Testudo galeata</i> Schoepff, 1792	IX
<i>Emys olivacea</i> Schweigger, 1812	III
<i>Pentonyx capensis</i> Duméril & Bibron, 1835	IX
<i>Pentonyx gehafie</i> Rüppell, 1835	new lineage X
<i>Pentonix americana</i> Cornalia, 1849	?
<i>Pelomedusa nigra</i> Gray, 1863	IX
<i>Pelomedusa gasconi</i> Rochebrune, 1884	III
<i>Pelomedusa galeata</i> var. <i>disjuncta</i> Vaillant & Grandidier, 1910	new lineage X
<i>Pelomedusa galeata damarensis</i> Hewitt, 1935	VIII
<i>Pelomedusa galeata devilliersi</i> Hewitt, 1935	IX
<i>Pelomedusa galeata orangensis</i> Hewitt, 1935	IX
<i>Pelomedusa subrufa wettsteini</i> Mertens, 1937	VIII

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TABLE S1. Used samples, GenBank sequences and their accession numbers.

TABLE S2. Primer sequences for mtDNA fragments for fresh samples. Nucleotides in brackets represent variable positions.

TABLE S3. Primer sequences and lengths of amplified PCR products of mtDNA fragments of the 12S, cyt *b* and ND4 genes for historical samples.

TABLE S4. PCR conditions for historical and fresh samples.

TABLE S5. Degree of overlap for individual mtDNA fragments yielding 251–252 bp of the 12S rRNA gene.

TABLE S6. Degree of overlap for individual mtDNA fragments yielding 319 bp of the cyt *b* gene.

TABLE S7. Degree of overlap for individual mtDNA fragments yielding 437 bp of the ND4 gene.

TABLE S8. Partitioning scheme and models selected by the Akaike Information Criterion in MrMODELTEST 2.3 (Nylander 2004).

The Supporting Information is available from the Dryad Repository using the link <http://dx.doi.org/10.5061/dryad.rd37p>

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